

The Cretaceous-Miocene genus *Lichenopora* (Bryozoa), with a description of a new species from New Zealand

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SYNOPSIS. The type species of the cyclostome bryozoan *Lichenopora* DeFrance, *L. turbinata* from the Eocene of France, is redescribed, allowing the concept of the genus to be revised. Colonies of *L. turbinata* consist of small, acute cones, unlike the majority of fossil and Recent species which have been since assigned to *Lichenopora*. Similar conical-pedunculate species of *Lichenopora sensu-stricto* range from the Lower Cenomanian to the Lower Miocene. The youngest is a species from the Parnell Grit (Burdigalian) of Auckland, New Zealand, described here as *L. parva* sp. nov.

INTRODUCTION

The bryozoan genus *Lichenopora* is well-known to bryozoologists (e.g. Alvarez 1993) and, indeed, to ecologists and natural historians in parts of the world where encrusting lichenopord bryozoans may be commonly associated with intertidal and shallow subtidal algae and rocky substrata (e.g. Sinel 1906; Rogick & Croasdale 1949; Morton & Miller 1968; Hayward 1988). About 40 nominal species of extant *Lichenopora* and over 100 fossil species have been described. As will be shown in this paper, however, *Lichenopora* should be restricted to a small suite of Cretaceous to Miocene species characterised, inter alia, by conical/pedunculate colonies.

The genus was proposed by DeFrance (1823) for three bryozoan species having autozooids clustered in short radiating crests not fused centrally to form a star. Two, one conical the other adnate, were Middle Eocene in age; the other, apparently also adnate, was Maastrichtian. Only the conical form, *L. turbinata*, was illustrated, and this was chosen by d'Orbigny (1853: 963), who discovered additional conical/pedunculate forms, as type species and representative of the genus: "Pour conserver cette coupe générique, nous prenons pour type la première espèce de [DeFrance], son *L. turbinata*, la seule qui présente plusieurs rangées de cellules aux lignées en cycles de la partie supérieure". Although d'Orbigny (1853) cited the genus as being characterised by the particular arrangement of autozooids in the colony, he did not include Recent adnate forms in it and, indeed, had previously diagnosed the genus as comprising "Bryozoaires coniques, fixées par le point du cône" (d'Orbigny 1852: 110), a viewpoint endorsed by Gregory (1909), who noted that even Busk (1859, 1875) did not attribute a single living species to *Lichenopora*. Instead, Busk (1859, 1875) used "*Discoporella*, Gray" (error for *Disporella* Gray, 1848) for the living, adnate forms, as did Smitt (1867) when proposing the family Lichenoporidae.

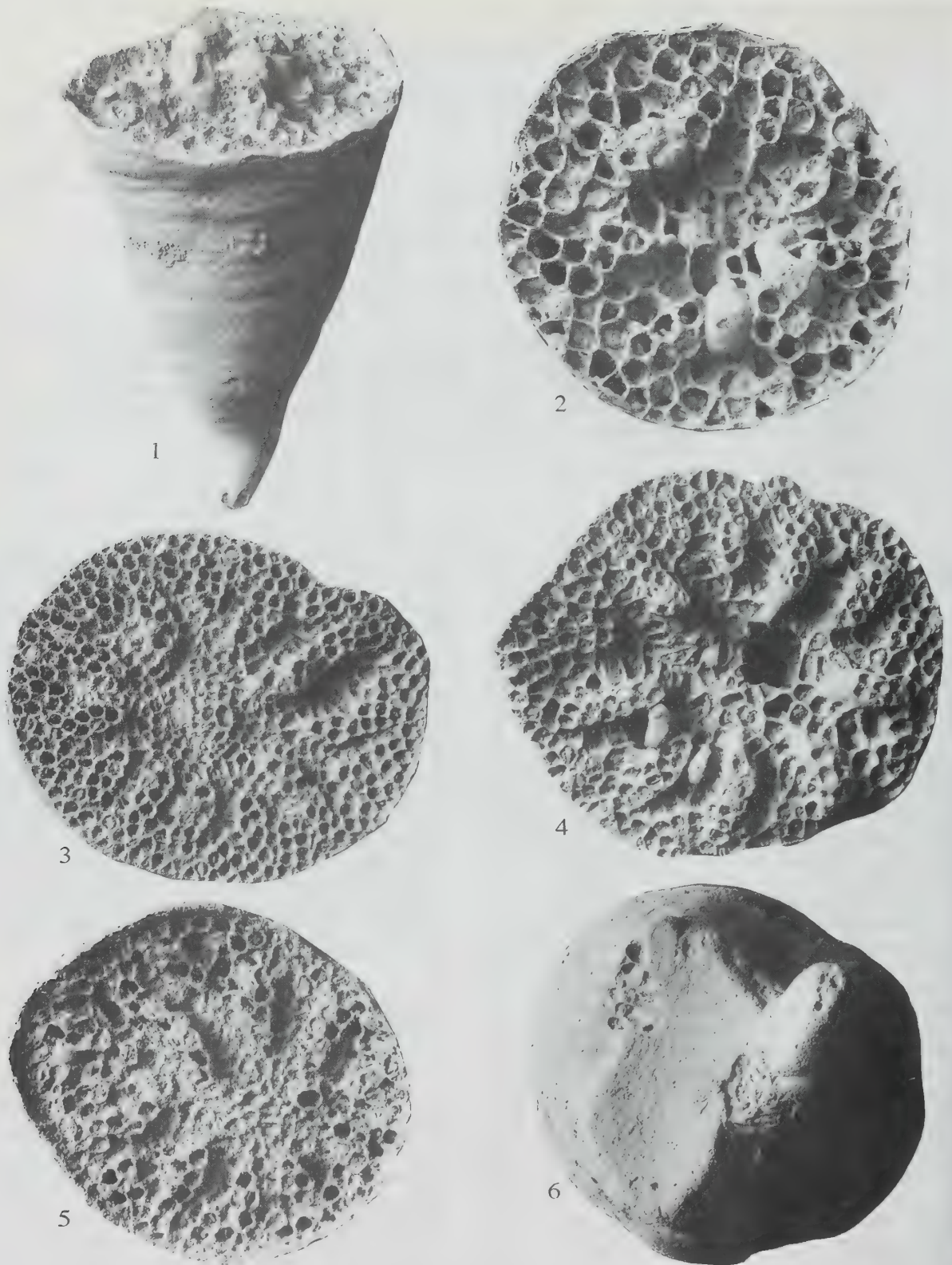
Prior to Gray's (1848) introduction of *Disporella*, some earlier authors (e.g., Milne Edwards 1838; Johnston 1847) had included living adnate lichenoporidae in *Tubulipora*, a branching adnate genus with calcified frontal walls and which is not closely related to

lichenoporidae. However, the French palaeontologist Michelin (1841–48), evidently following DeFrance's (1823) wider view of the genus, included adnate forms in *Lichenopora*. So too did Reuss (1846). Whereas Smitt still used the combination *Discoporella verrucaria* up to 1868, he later changed his view of generic relationships, attributing *D. verrucaria* to *Lichenopora* without explanation (Smitt 1878a,b). This appears to have persuaded Thomas Hincks, for, in his very influential work *British Marine Polyzoa* (Hincks 1880), he used the genus *Lichenopora* for *D. verrucaria* (and other living adnate species including *D. hispida*), citing Smitt (1878a) in his synonymy as the only previous author to use this combination. The use of *Lichenopora* for all living adnate forms continued until Borg (1933) reintroduced *Disporella* Gray, 1848 as a subgenus of *Lichenopora*, then as a full genus (Borg 1944) to accommodate the type species (*D. hispida* Fleming) and some other species, while continuing to use *Lichenopora* for *Madreporella verrucaria* Linnaeus and related species. Sabri (1988) pointed out that Brood (1972) was the first palaeontologist to use *Disporella* for fossil species.

SYSTEMATIC PALAEOLOGY

Specimen repositories and abbreviations: BMNH, The Natural History Museum, London; IGNS, Institute of Geological & Nuclear Sciences, Hutt City (formerly New Zealand Geological Survey, NZGS); MNHN, Muséum National d'Histoire Naturelle, Paris.

The species described were all studied by scanning electron microscopy (SEM), using type and/or topotypic specimens. Most SEM was carried out on uncoated specimens in an environmental chamber attached to an ISI ABT-55 scanning electron microscope. This generated back-scattered electron images in contrast to the secondary electron images which are used in conventional SEM of coated specimens. All figures are uncoated scanning electron micrographs. Morphometric determinations were made using an eyepiece micrometer affixed to a Wild M7 binocular microscope, or from SEM micrographs where necessary.



Figs 1-6 *Lichenopora turbinata* DeFrance, 1823. Eocene, Manche, France. **1**, MNHN, Canu Collection, R. 53447, M. Lutetian, Orglandes, profile of conical colony, $\times 18$. **2**, BMNH BZ 3163, Hauteville, disc surface of small infertile colony, $\times 26$. **3-6**, MNHN, d'Orbigny Collection, B.50246, 'Parisien', Orglandes; **3**, disc of colony with well-developed autozooidal rays, $\times 13$; **4**, disc of fertile colony, $\times 15$; **5**, disc of another colony with raised edges, $\times 15$; **6**, underside of colony with an extensive basal attachment to an unpreserved substratum represented by a mould bioimmuration, $\times 16$.

Order **CYCLOSTOMATIDA** Busk, 1852
 Suborder **RECTANGULINA** Waters, 1887
 Family **LICHENOPORIDAE** Smitt, 1867
 Genus *LICHENOPORA* DeFrance, 1823

TYPE SPECIES. *Lichenopora turbinata* DeFrance, 1823, subsequently designated by d'Orbigny (1853: 963); Eocene (Lutetian), France.

DIAGNOSIS. Colony an even, acute cone, tapering basally, or with the cone expanded outward laterally and supported by a short peduncle; cone sides comprising a basal exterior wall with or without accessory kenozooidal prop-like processes. Zooids free-walled, tubular and straight in longitudinal section, opening on subcircular frontal disc; both autozooids and kenozooids arranged quincuncially near the edge of the disc, with older autozooids tending to become grouped in several elevated radial series that converge at or near the centre of the disc. Brood chamber located centrally, but may have lobes extending into interradial areas between autozooidal rows; roof comprising an interior wall typically overgrown by the walls of shallow kenozooids that develop on its surface. Ooeciopore relatively large, situated near the centre of the disc.

DISTRIBUTION. Cretaceous (Lower Cenomanian) – Eocene (Lutetian) of Europe; Lower Miocene (Burdigalian) of New Zealand.

Lichenopora turbinata DeFrance, 1823 Figs 1–10

- 1823 *Lichenopora turbinata* DeFrance: 257, pl. 46, figs 4, 4a.
 1852 *Lichenopora turbinata* DeFrance; d'Orbigny: 963.
 1909 *Lichenopora turbinata* DeFrance; Canu: 138, pl. 17, figs 13–15.
 1953 *Lichenopora turbinata* DeFrance; Bassler: 73, fig. 38.1.
 1956 *Lichenopora turbinata* DeFrance; Balavoine: 321.
 1970 *Lichenopora turbinata* DeFrance; Labracherie: 37, pl. 6, figs 8–9.
 1988 *Lichenopora turbinata* DeFrance; Sabri: 141.

MATERIAL. MNHN, d'Orbigny Collection, B.50246 (a–f), Eocene, 'Parisien', Orlandes, Manche, France; MNHN, Canu Collection, R. 53447, Eocene, M. Lutetian, Orlandes, Manche, France; BMNH BZ 3163, Eocene, Hauteville, Manche, France, C. Lyell Collection, presented by T. R. Jones, 1896.

The type material of this species is thought to be lost: none of the MNHN specimens seem to represent that figured by DeFrance.

DESCRIPTION. Colony an inverted cone (Fig. 1), up to 4.7 mm high and 3.3 mm diameter, the cone diverging at an angle of about 45°. Apical end of cone evenly tapered and straight, or the apex somewhat deflected at an angle from the axis; frequently broken, showing a dozen or so zooidal tubes in transverse section, each tube 0.09–0.13 mm diameter. Sides of cone formed of exterior wall (the upturned basal wall of the colony), more or less smooth textured; in profile, the sides of the cone may be nearly straight or very gently undulose; light concentric or subconcentric growth banding is typical. Supportive kenozooidal props have not been observed, but some colonies bear grooves or planar areas down one side of the cone or transversely near the apex, representing bioimmurations of a substratum to which the cone was attached laterally (Fig. 6). Disc circular or elliptical (Figs 2–5) and slightly depressed beneath the level of the rim in well-preserved specimens.

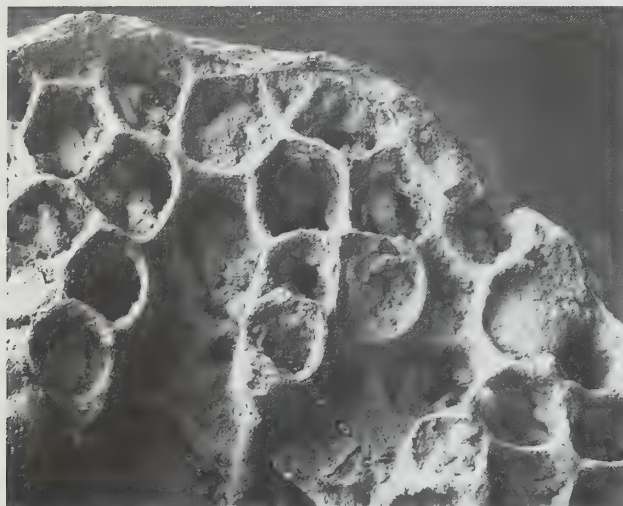
Zooidal apertures near the outer (distal) margin of disc are arranged quincuncially (Fig. 7), have more or less equal diameter (0.14–0.17 mm centre-to-centre spacing), and are polygonal in shape; there is no obvious distinction between autozooidal and kenozooidal apertures in these submarginal areas, but the outermost apertures beyond autozooidal rays are presumed to have been autozooids. In mature colonies with brood chambers, autozooids are arranged in elevated biserial rays with apertures alternating (Figs 3–5, 8), each aperture elliptical, up to 0.19 mm in diameter and elongated along the axis of the ray; there are up to 10 such rays, each with 4–6 pairs of autozooids, terminating abruptly near the concave centre of the disc. Between the rays are at least two rows of kenozooidal apertures. In immature colonies (i.e., smaller colonies without a visible brood chamber), the autozooidal rays are less distinct and shorter (Fig. 2), comprising 2–4 pairs of autozooids only, with some of the autozooids unpaired.

The disc centre is composed of kenozooids which may become covered by a brood chamber with lobes extending between the autozooidal rays (Fig. 4). The roof of the brood chamber appears to be sparsely porous and is overgrown by a network of ridges that define shallow kenozooidal chambers (alveoli). The prominent ooeciostome (Fig. 9), located at or near the centre of the disc, comprises a short broad tube with an oval ooeciopore (Fig. 10), 0.11–0.17 mm × 0.23 mm in diameter, roughly twice the width of an autozooidal aperture.

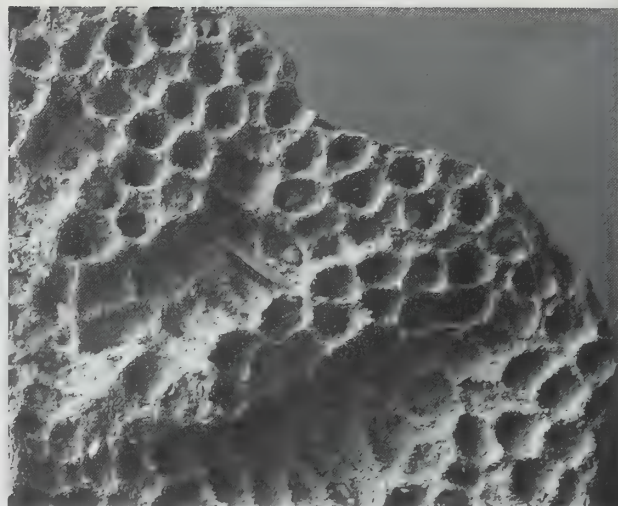
REMARKS. Canu (1909) illustrated *L. turbinata* using several light micrographs, of which plate 17, fig. 14 was reproduced as a mirror-image line drawing in Bassler's (1953: fig. 38.1) bryozoan *Treatise*. It is unfortunate that Bassler did not also illustrate *L. turbinata* in profile, for it has not generally been appreciated that the type species of *Lichenopora* is conical. According to Canu, the elongate conical form is rare, and shorter colonies are more commonly found; however, the only colony he figured in profile is steeply conical. Similarly, the colony shown in profile by Labracherie (1970: pl. 6, fig. 9) is also a high cone, and all of the material available to us had the same form. Kenozooidal props have not been described in the literature and were not encountered in our material.

A few remarks on the ecology of *L. turbinata* are possible. Although DeFrance (1823) illustrated a slight expansion at the apex of the cone and a flattened base, indicating a direct and limited attachment to a substratum, the groove-like or planar bioimmurations (Fig. 6) on the sides of a few colonies are evidence of a more extensive lateral attachment in some instances. Inasmuch as the molluscan fauna associated with *L. turbinata* at the localities where it is found in the Paris Basin is characteristic of seagrass beds (Jon Todd & Didier Merle, pers. comms, December 1994), it is possible that colonies lived attached to seagrass. Associations between bryozoans and sea-grasses date back to the Maastrichtian (Voigt 1981), and are well-known from the Mediterranean at the present-day. For example, Hayward (1975) noted more than 30 bryozoan species, including one obligate epiphyte, living on *Posidonia oceanica* from Chios, Greece. However, none of these species have conical colonies like those of the Eocene *L. turbinata*, and fossil examples of seagrass associations from the Maastrichtian (Voigt 1981) and Eocene (Ivany *et al.* 1990) similarly lack conical colonies, although they do include lichenoporidae.

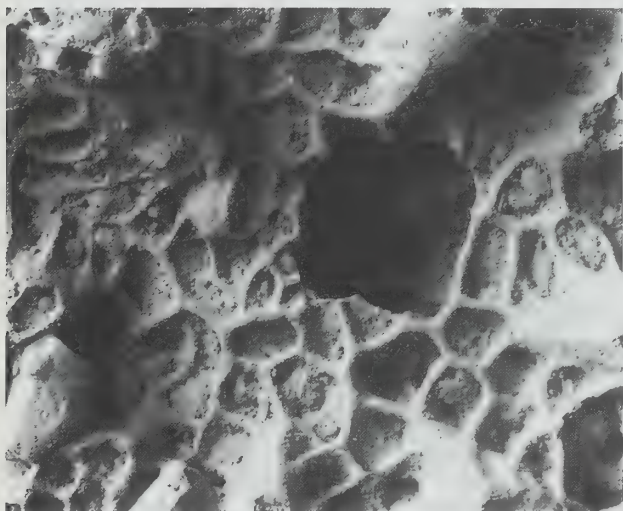
DISTRIBUTION. Eocene of France: Lutetian of the Paris Basin (Canu 1909), Middle-Upper Eocene of northern Aquitaine (Labracherie 1970).



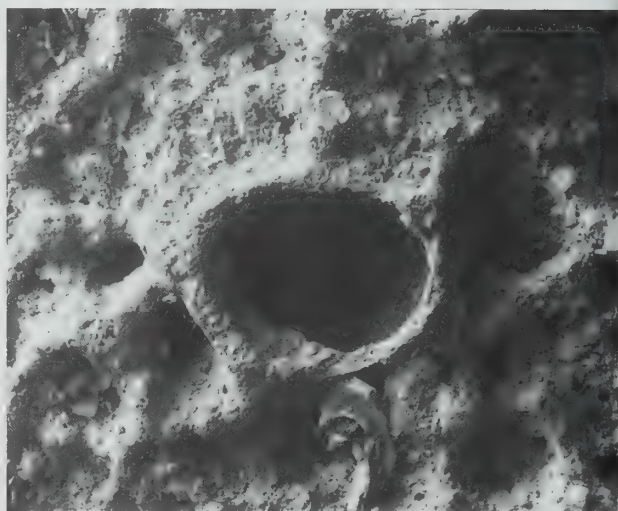
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Figs 7–10 *Lichenopora turbinata* DeFrance, 1823, Eocene, Manche, France. **7**, BMNH BZ 3163, Hauteville, edge of disc showing initial quincuncial arrangement of zooids, $\times 73$; **8–10**, MNHN, d'Orbigny Collection, B.50246, 'Parisien', Orglandes; **8**, autozooidal rays separated by grooves containing kenozooids, $\times 43$; **9**, centre of a fertile colony with broken brood chamber roof to the left of which is an oocystostome, $\times 60$; **10**, oocypore from the colony depicted in Fig. 5, $\times 150$.

***Lichenopora parva* sp. nov.**

Figs 11–15, 17–20

HOLOTYPE. IGNS BZ 181, Miocene, Otaian (= Burdigalian), Waitemata Group, East Coast Bays Formation, Parnell Grit, Faulkner Bay, Manukau Harbour, Auckland, New Zealand (Grid Reference R11/654728), collected by D. P. Gordon & P. D. Taylor, March 1996. New Zealand Fossil Record Number R11/f197.

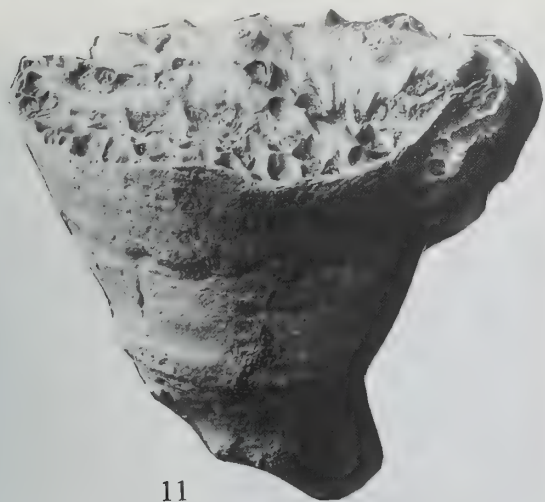
PARATYPES. IGNS BZ 182–3; BMNH BZ 3505–7; details as for holotype.

DIAGNOSIS. A small *Lichenopora*, not more than 2.5 mm high, the cone angle 45–85°; kenozooidal props present or absent; tubercle-like thickenings of zooidal walls near the disc centre.

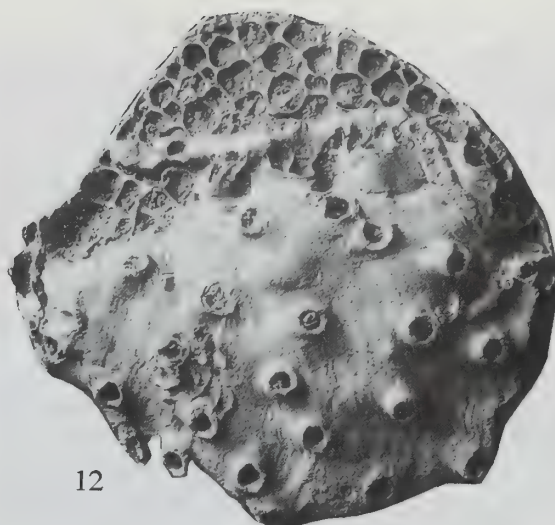
DESCRIPTION. Colony conical (Figs 11, 13–15, 17), tiny, about as

wide as high, preserved size not exceeding 2.5 mm high and 3.4 mm in diameter, the angle of the cone 45–85°. Outer (basal) surface of cone textured with faint concentric growth banding; cone apex symmetrical, rounded, or slightly irregular according to the substratum. Short, hollow kenozooidal props (Fig. 15) occur on some specimens, as many as 3 on one side, or these may be entirely absent. Disc nearly circular in outline, surface significantly depressed below the rim in well-preserved material (Fig. 14). Disc surface convex, rising to short prominences near the centre.

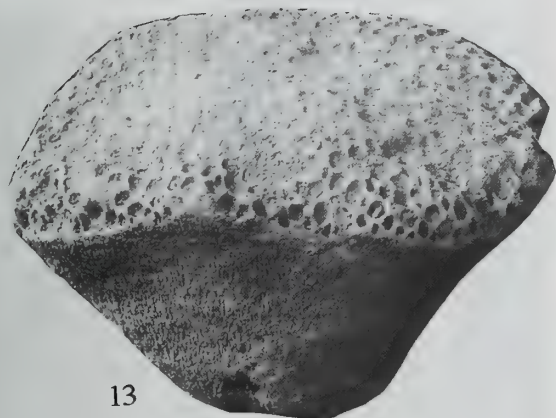
Zooids arranged in irregular quincunx, with considerable variation in apertural diameter, size generally increasing centripetally; the largest apertures (up to 0.20 mm in diameter) are assumed to be autozooidal, the smallest kenozooidal (i.e. alveoli) or new buds (Figs 19–20). Autozooids not clearly arranged in rays (Fig. 18).



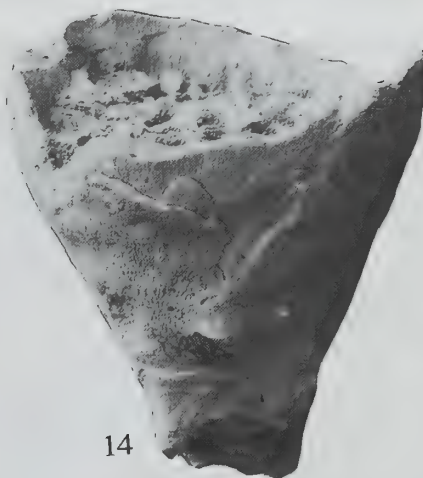
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Figs 11–16 *Lichenopora parva* sp. nov., Miocene, Otaian, Parnell Grit, Faulkner Bay, Auckland, New Zealand. **11–12**, BMNH BZ 3505; **11**, profile of conical colony, $\times 38$; **12**, surface of disc overgrown by a sheet-like and a uniserial tubuliporine cyclostome, $\times 40$. **13**, BMNH BZ 3506, large conical colony with poorly-preserved surface, $\times 22$. **14**, IGNS BZ 183, tiny cone with disc surface strongly depressed, $\times 40$. **15**, BMNH BZ 3507, conical colony with the broken base of a prop (depicted upside-down because of constraints in SEM stage tilt), $\times 32$. **16**, *Lichenopora pedunculata* Voigt, 1989, Cretaceous, Lower Cenomanian, Mülheim, Westfalia, Germany, BMNH D58007, underside of conical colony with broken stalk and the base of a prop, $\times 27$.

Broken apertural spines present on the proximal sides of autozooidal apertures in the least abraded specimen (Fig. 20). Centre-to-centre-spacing of the largest-diameter zooids is 0.12–0.20 mm. Stout tubercle-like thickenings of the zooidal walls are commonly developed near disc centre (Fig. 19), sometimes attaining the diameter of an autozooidal aperture.

Brood chamber not seen at disc surface; however, a questionable brood chamber was visible in a sectioned specimen below the disc surface.

REMARKS. *Lichenopora parva* differs from *L. turbinata* Defrance in its consistently smaller size, tubercle-like thickenings of the zooidal walls and lack of arrangement of autozooids into radial rays, and from other related conical/pedunculate species (see below) in the asymmetrical placement of the kenozooidal props and smaller cone angle, apart from differences in geographical distribution and stratigraphic age. In colonial morphology, the species that most closely resembles *L. parva* is *L. pedunculata* Voigt, 1989 from the Lower Cenomanian of Westfalia, Germany. This Cretaceous species has small conical colonies of almost the same form, not exceeding 3 mm height and diameter. Most strikingly, it also has kenozooidal props (Fig. 16) which appear to occur on all specimens, with 2–6 props distributed around the sides of the cone. However, autozooids are arranged in uniserial rays in *L. pedunculata*.

None of the six species of 'Lichenopora' recorded by Waters (1887) from the Cenozoic of New Zealand have conical colonies.

The mode of attachment during life of this tiny species is not known as the proximal cone apex is always missing, although evidence of supportive props suggests that secondary attachments to the substratum were developed. More intact props have been figured in *L. pedunculata* by Voigt (1989, pl. 7, figs 3, 4, 7, 8). One colony of *L. parva* is partly overgrown by a sheet-like tubuliporine cyclostome that started life on the side of a cone and then grew over the rim to cover virtually the entire disc surface (Fig. 12), and a uniserial tubuliporine.

The new species has been recorded only from the Parnell Grit. The Parnell Grit comprises several beds of Early Miocene (Otaian = Burdigalian) volcanics interbedded with bathyal flysch, and each bed is interpreted as a deposit formed by a subaqueous gravity flow (submarine lahar) which picked up bryozoans as it passed over the shallow shelf (Ballance & Gregory 1991). Consequently, the colonies of *L. parva* are allochthonous and their original habitat is unclear.

DISTRIBUTION. Miocene: Otaian (= Burdigalian), Auckland, New Zealand.

DISCUSSION

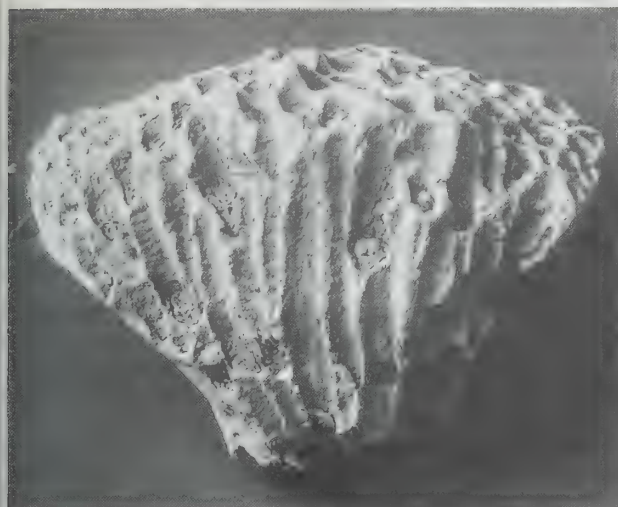
Several pedunculate Cretaceous species superficially resembling the type and other conical species of *Lichenopora* were described and illustrated by d'Orbigny (1853). Using the nomenclature in d'Orbigny's atlas of plates (pls 645, 646), they include: *Lichenopora compressa*, *L. elatior*, *L. irregularis*, *L. organisans*, *L. pocillum*, and *L. tuberculata*. Of these, *L. tuberculata* appears to be a tubuliporine; *L. organisans* was removed by Pergens (1890) to *Apsendesia* Lamouroux, another tubuliporine, and Pergens synonymised *L. compressa* with *L. pocillum*. We have not examined type or reliably determined material of *L. pocillum*, *L. elatior*, or *L. irregularis*, but have been able to study using SEM a possibly related species, *Defrancia cariosa* von Hagenow, 1851, which d'Orbigny (1853) included in *Lichenopora*. This is a robust pedunculate form that

superficially resembles *Lichenopora*, but has vertically stacked brood chambers. Without further revision of all of these forms, which require the brood chamber for taxonomic certainty, we cannot suggest an alternative genus. *Lichenopora defranciana* Michelin, 1845, also mentioned by d'Orbigny, is pedunculate and very like *Lichenopora* as here defined in the characters of the disc, but we have not encountered brood chambers in museum specimens and cannot comment further on its affinities. (It should be noted that, in his text, d'Orbigny (1853) used *Discocavea* (type species *L. irregularis*) for several species attributed to *Lichenopora* in his plates.) *Lichenopora convexa* Canu, 1909 from the Lutetian of the Paris Basin is a true *Lichenopora*. It forms small conical colonies ca. 2 mm high and up to in 3.8 mm diameter, with an apparent cone angle of 100° based on the single colony illustrated in profile by Canu (1909). In addition to the cone apex by which the species appears to have been attached in life, Canu described a prop on one side of some colonies, giving the appearance of two basal supports. Autozooids are arranged in uniserial rows, unlike the biserial arrangement found in *L. turbinata*.

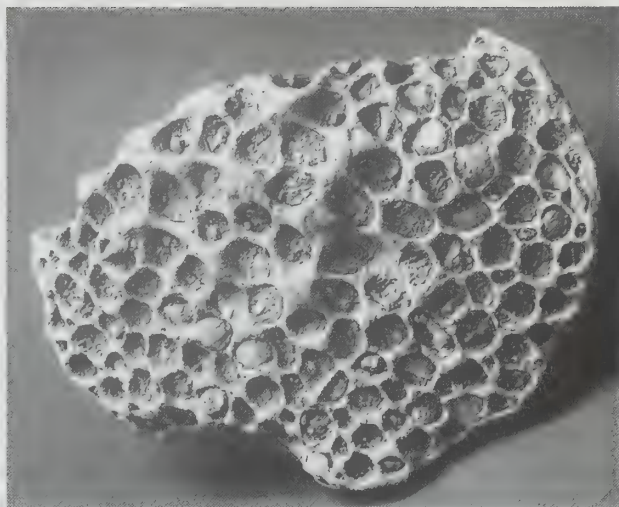
From all the material that we have seen, and from the literature, we conservatively interpret *Lichenopora* to include only conical and some conical-pedunculate species, e.g. Lower Cenomanian *L. pedunculata* Voigt, Lutetian *L. convexa* Canu and *L. turbinata* Defrance, Burdigalian *L. parva* sp. nov., and probably Danian-Lutetian *L. defranciana* (plus others of similar form that require restudy). All of these species are characterised by the possession of an erect, conical or conical-pedunculate colony form. This colony-form is regarded as an apomorphy relative to the more normal adnate discoidal colony forms found in other lichenoporidae and some closely-related cerioporines (e.g. *Favosipora*). Additionally, although not yet known in the type species, most species have supportive kenozooidal props. These props are not present in every colony of the species that can produce them, implying some phenotypic plasticity. Importantly, such props are not known in any modern species – there are instances in which some modern lichenoporidae (e.g., expansive colonies of some *Disporella* species) are unable to be entirely adnate to a highly irregular substratum. In such cases, concentric ridges of calcification from the basal wall, representing earlier growth bands, "bend" into a concavity of the substratum while the general trend of the basal wall continues at right angles to the bend. These structures are solid, however, and do not contain kenozooidal chambers. Thus kenozooidal props would also appear to be an apomorphy characterising *Lichenopora sensu stricto*.

Recent species attributed to *Lichenopora* are strictly adnate (e.g. Alvarez 1993). Within 1–3 zooidal generations from the ancestrula, the proximal colony margin folds back over the protoecium to adhere immediately to the substratum, establishing evenly circumferential colony expansion. In some adnate species previously attributed to *Lichenopora*, especially when attached to erect bryozoans where space is lacking for lateral expansion, the so-called basal lamina or colony margin can curve upwards considerably, resulting in a calyciform colony. In longitudinal section, however, such colonies are still centrally adnate and broader-based and do not resemble the strictly conical forms with their narrower points of attachment to the substratum. A priori, it would seem logical to derive pedunculate and conical colonies from adnate forms by diminishing the area of attachment centrally.

The question arises as to the generic placing of the numerous Cenozoic and Recent adnate species previously attributed to *Lichenopora*. For these, the genus *Patinella* Gray, 1848 (type species *Madrepora verrucaria* Linnaeus) is available, assuming that brood-chamber construction is indeed different from that of *Disporella* Gray, 1848 (see Schäfer 1991).



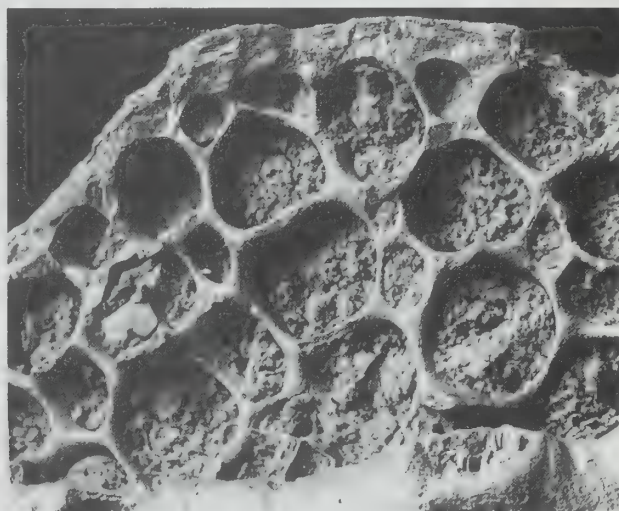
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Figs 17–20 *Lichenopora parva* sp. nov., Miocene, Otaian, Parnell Grit, Faulkner Bay, Auckland, New Zealand. **17–19**, IGNS BZ 181, **holotype**; **17**, longitudinally fractured colony showing tubular zooids, $\times 35$; **18**, disc surface, $\times 35$; **19**, variably-sized zooidal apertures and tubercle-like wall thickenings, $\times 85$. **20**, BMNH BZ 3505, well-preserved disc surface showing apertural spines, $\times 145$.

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